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Primary Succession in Glacier Forelands: How Small Animals Conquer New Land Around Melting Glaciers

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1. Introduction

An easily observed effect of global warming is the gradual melting of glaciers in different parts of the world. Large areas of barren, pristine ground are left open for colonisation of various life forms (Fig. 1). From an ecological point of view, glacier forelands are interesting because they illustrate nature's ability to recover from severe disturbance. Since the successive development of communities starts without previous life forms, it is a primary succession. In contrast, a secondary succession starts with a species assemblage already present, for instance on a forest patch after clear-cutting. While the botanical succession in glacier forelands has been well studied, the parallel zoological succession is less described and understood. Which animal species are pioneers, what properties make them pioneers, how fast does species number increase, and how do plants and animals interact during succession? An ecological understanding of primary succession is not only of scientific interest, but also helps us to predict future ecosystems in areas freed from the ice cover.

2. Glacier forelands: Nature's ecological laboratory

In some glacier forelands, glaciologists have followed the varying position of the ice edge during long time, sometimes supported by old photographs. The age of certain characteristic moraines can, for instance, be well dated, and the age of sites between may be estimated. Several European glaciers had a maximum size at the end of the "Little Ice Age", which in Norway ended around A.D. 1750 with well-marked moraines. Forelands with dated sites up to 250 years age represent unique ecological laboratories for understanding nature's ability to conquer new land.

Ideally, a primary succession should be studied by following the gradual changes in flora and fauna in a fixed site over long time, from being newly freed from the ice cover, to having achieved a stable community structure. This is rarely possible, and the usual way is to substitute time with space, using plots with known age to estimate the future biological status of newly exposed land. The sequence of dated study plots in the foreland, illustrating the succession on a given site over time, is called a chronosequence.



Fig. 1. Foreland at the Midtdalsbreen glacier snout, a part of the Hardangerjøkulen glacier in central south Norway. Photo: Sigmund Hågvar.

The ideal situation in a chronosequence is that the glacier has retreated at a constant speed, that climate conditions have been stable, and that the exposed ground has not been subject to reworking, for instance by glacier rivers. If temperature has been especially high during the last decades, the youngest sites may have developed faster than older sites did in their early phases of succession. Also, the source sites from which colonising organisms derive, can be influenced by climate change. A perfect chronosequence in all respects is hard to find, but certain forelands contain good historical information and well dated sites.

The botanical changes from a pioneer flora to a closed and stable plant community has been described in various glacier forelands, both in Norway (Matthews & Whittaker, 1987; Matthews, 1992; Vetaas, 1994, 1997), in the Austrian Alps (Moreau et al., 2005; Raffl, 1999; Raffl et al., 2006), and in Alaska (Chapin et al., 1994). Especially during the last decade, increased insight has also been given in the zoological succession along receding glaciers, from three different geographical areas in Europe: Svalbard, the Alps, and Norway. The invertebrate succession in two glacier forelands in Svalbard was described by Hodkinson et al. (2004). In Austria, early faunistic studies in glacier forelands by Janetschek (1949, 1958) and Franz (1969) were followed by Gereben (1994, 1995) on carabid beetles, and Paulus & Paulus (1997) on spiders. Recently, the foreland of the Austrian Rotmoos glacier has been under intense study, including invertebrate succession (Kaufmann, 2001, 2002; Kaufmann et

al., 2002; Kaufmann & Raffl, 2002). In Italy, Zingerle (1999) studied spiders and harvestmen in the Dolomites, and Gobbi et al. (2006a,b, 2007) have described epigeal arthropod succession in a glacier foreland in Central Italian Alps.

From southern Norway, three master/PhD theses based on pitfall trapping in glacier forelands focused mainly on surface active beetles and spiders (Alfredsen, 2010; Bråten & Flø, 2009; Vater, 2006). The other Norwegian faunistic studies in glacier forelands dealt with soil living mites (Acari) (Hågvar et al., 2009; Seniczak et al., 2006; Skubala & Gulvik, 2005) or springtails (Collembola) (Hågvar, 2010). Time has come to summarize and compare the invertebrate succession in these different geographical areas, looking for similarities, differences, and mechanisms.

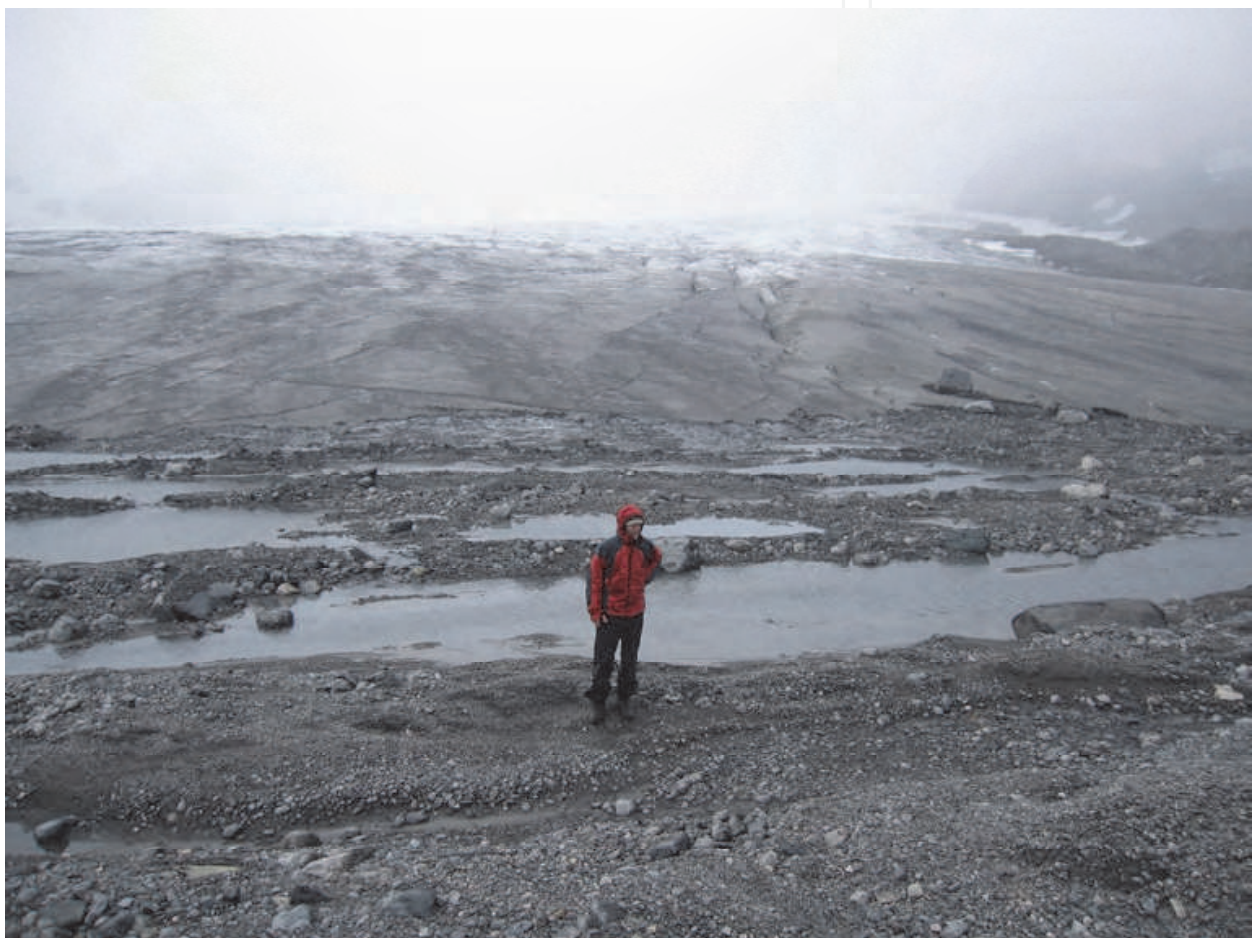


Fig. 2. Midtdalsbreen glacier snout in Norway, August 2010: Behind the author, a 20 m broad belt of barren ground was freed from ice during this summer. Photo: Daniel Flø.

3. Life on barren ground: The pioneer animals

Several invertebrate groups are present on barren, vegetation-free ground close to the glacier boarder (Figs. 2-3). Typical representatives are springtails (Collembola) and mites (Acari), which are collectively named microarthropods, as well as beetles (Coleoptera), spiders (Araneae) and harvestmen (Opiliones). Since there is no organic layer, the pioneer invertebrates are surface active species, but they can find shelter in the crevices among stones, gravel and sand grains.



Fig. 3. Pitfall traps (with visible lids) on this barren, three year old moraine trapped many species of spiders, beetles, springtails and mites. Photo: Sigmund Hågvar.

3.1 Pioneer springtails (Collembola)

Table 1 lists pioneer springtails collected close to Midtdalsbreen glacier snout, which is a part of Hardangerjøkulen glacier in alpine south Norway. Pitfall catches from young ground illustrate the relative surface activity at ages 3, 36 and 47 years, while flotation a few meters from the ice edge (age 0 years) proved the presence of two species on freshly exposed ground (Fig.2). One of these, *Agrenia bidenticulata*, is characteristic for cold, moist habitats in arctic and alpine areas (Fjellberg, 2007). This specialized species disappeared already after 30-40 years, at which time two generalist species dominated the surface activity: *Lepidocyrtus lignorum* and *Isotoma viridis*. Table 1 also shows an intermediate phase after 3 years, where the surface activity was dominated by the large, sphere-formed species *Bourletiella hortensis*, and as much as eight species were already present. This case illustrates the great colonisation ability of springtails, how both specialists and generalists participate, and how the community structure may undergo rapid changes during the first few years. Although the Collembola fauna is different in forelands on Svalbard (Hodkinson et al., 2004) and in the Austrian Alps (Kaufmann et al., 2002), the colonisation pattern has certain features in common in these three geographical sites: Springtails were among the earliest colonisers with a documented presence after only 2-4 years, and Isotomidae and Hypogastruridae were often pioneer families.

Age (year)	0	3	32-36	41-47
Sampling method	Flotation	Pitfall	Pitfall	Pitfall
<i>Agrenia bidenticulata</i>	84.6	24.7		
<i>Desoria infuscata</i>	15.4	1.5	6.5	
<i>Bourletiella hortensis</i>		59.9	1.1	
<i>Isotoma viridis</i>		5.2	28.3	21.3
<i>Lepidocyrtus lignorum</i>		0.4	50.0	65.3
<i>Desoria olivacea</i>		8.0	8.7	4.5
<i>Desoria tolya</i>		0.2	4.3	3.0
<i>Ceratophysella scotica</i>		0.1	1.1	6.1
NUMBER OF ANIMALS	26	1465	92	66

Table 1. Collembola sampled from young sites near the Midtdalsbreen glacier snout, Norway. Percentage dominance of various species are given. Pitfall catches illustrate surface activity. Flotation was used close to the ice boarder.

3.2 Pioneer mites (Acari)

Pitfall trapping near Midtdalsbreen glacier snout in Norway documented a considerable surface activity of small mites after 3 years, belonging to Actinedida (earlier called Prostigmata). Pitfalls and soil samples at 32-47 year age showed that other mite groups had then been added: Oribatida and Gamasina (Hågvar et al., 2009). Also on Svalbard and in the Alps, mites were recorded after only 2-4 years (Hodkinson et al., 2004; Kaufmann et al., 2002). Interestingly, the small, generalist oribatid species *Tectocephus velatus* was a pioneer species both at Midtdalsbreen, in another foreland at Jostedalsbreen glacier in south Norway (Skubala & Gulvik, 2005), as well as in two forelands on Svalbard (Hodkinson et al., 2004). Moreover, the species was found to be a characteristic pioneer on vegetation-free post-industrial dumps in Poland (Skubala, 2004). Also certain small species of the oribatid family Brachychthoniidae were early colonisers both in Norwegian forelands and in the industrial dumps. Maybe the pioneer community is more predictable for mites than for springtails in a primary succession.

3.3 Pioneer spiders (Araneae)

Also spiders are among the first colonisers on barren ground, both on Svalbard, in Norway and in the Alps. Pioneer spiders often belong to the family Lycosidae (wolf spiders) or Linyphiidae (sheet web spiders). Wolf spiders are robust and agile night hunters with good eyesight and hunt without constructing a web. In the Italian Alps, the wolf spider *Pardosa saturator* is in fact living among debris on the glacier surface (Gobbi et al., 2006a). In the foreland of the Austrian Rotmoos glacier this species is a typical pioneer together with *Pardosa nigra* (Kaufmann, 2001). In several South-Norwegian glacier forelands, the genus *Pardosa* was recognized as a pioneer by Vater (2006). The species *Pardosa trailli* (Fig. 4) was identified both in several young forelands in the Jotunheimen area by Vater (2006), and close to the Hardangerjøkulen glacier (Bråten & Flø, 2009). The large group of sheet web spiders are small, delicate animals which weave horizontal, sheet like webs under which they are hanging. Above the sheets the spider inserts strands, into which insects fly and fall onto the web. In two Svalbard forelands, *Erigone arctica* was found after 16 years (Hodkinson et al., 2004). The same species is also a pioneer at the

Hardangerjøkulen glacier in South Norway, being recorded on a three year young moraine (Bråten & Flø, 2009). A related species, *Erigone tirolensis*, is a common pioneer at the Hardangerjøkulen glacier and in the Rootmostal foreland in Austria (Bråten & Flø, 2009; Kaufmann, 2001).



Fig. 4. The large and fast-running wolf spider *Pardosa trailli* is a pioneer species in Norwegian glacier forelands. Photo: Sigmund Hågvar.

3.4 Pioneer harvestmen (Opiliones)

Mitopus morio is a large and very active species which is common on newly exposed ground, less than 20 years old, in several South-Norwegian forelands studied by Vater (2006). Bråten & Flø (2009) found it abundantly on a three year old moraine close to Hardangerjøkulen glacier in south Norway. Together with *M. glacialis*, the species is also a pioneer in the Alps (Kaufmann, 2001).

3.5 Pioneer beetles (Coleoptera)

While beetles were absent in the forelands studied on Svalbard (Hodkinson et al., 2004), they belonged to the pioneers in all studies in Norway and the Alps. A characteristic picture is that species within the family Carabidae are present on barren ground close to the glacier. Moreover, certain genera, and even species, are common pioneers in these two geographical areas. Typical genera in this respect are *Nebria*, *Amara* and *Bembidion*. In South Norway,

Vater (2006) found the following carabid species in various foreland sites younger than 20 years: *Amara alpina*, *A. quenseli*, *Nebria nivalis*, and *Bembidion fellmanni*. The same species were pioneers close to Hardangerjøkulen glacier, except for another *Bembidion* species: *B. hastii* (Bråten & Flø, 2009, Fig. 5). In the Austrian Alps, Kaufmann (2001) recorded *Amara quenseli*, four *Nebria* species and a *Bembidion* species as early colonisers, and also Gobbi et al. (2006a) recorded *A. quenseli* as a pioneer species in the Italian Alps.



Fig. 5. *Bembidion hastii*, a pioneer predatious Carabidae beetle in Norwegian glacier foreland. Photo: Oddvar Hanssen.

3.6 Other pioneer groups

On a four year old barren moraine at Hardangerjøkulen glacier in South Norway, extraction of soil samples revealed the presence of Rotatoria and at least five different Nematoda genera. Tardigrada was found close to a single plant of *Poa alpina* (Christer Magnusson, pers. comm). In Austria, Kaufmann et al. (2002) found both Nematoda and Enchytraeidae in soil samples younger than 40 years. On Svalbard, Hodkinson et al. (2004) recorded larvae of terrestrial Chironomidae after 2 years and Enchytraeidae after 37 years.

4. Dispersion: How to get there?

Pioneer invertebrate species must be good dispersers, but our knowledge in this field is limited. The easiest dispersion would be by air, either by active flight, by passive wind transport, or a combination. On Svalbard, areal dispersal of invertebrates over the foreland of Midtre Lovénbreen glacier was studied by Coulson et al. (2003). Large numbers of Diptera, Hymenoptera and Araneae were caught in water and sticky traps, some only 15 m

from the glacier snout on 2 year old ground. Sticky traps were placed either just above ground level, or at a height of 1 m. It was concluded that spiders caught 1 m above ground must have been aerially dispersed. The actual spider family, Linyphiidae, is known for their ability to fly by wire, called "ballooning". By raising the abdomen and gradually releasing a thread in the breeze, the spider is finally lifted upwards and can be blown very far away. Holm (1958) suggested that many spider species on Svalbard had originally arrived from Greenland as aerial plankton. The airborne Diptera and Hymenoptera in the glacier foreland represented a food source for the spiders. Another interesting observation was that more than 95 % of the animals caught in sticky traps were taken close to the ground, and very few at 1 m height. The vast majority of animals were dispersing at, or below, 0.25 m. Furthermore, animals were trapped from all directions, despite some prevailing wind directions during the study. It was concluded that these arctic insects appear to make flights of short duration and remain close to the ground where wind velocities are considerably reduced and air temperatures elevated. This behaviour enables them to perform directional flight largely independent of wind direction (Coulson et al., 2003).

Although several springtails and mites are early colonisers on Svalbard, Coulson et al. (2003) did not catch these groups in the sticky traps. Later, Mangnussen (2010) achieved some springtails and mites in water traps on Svalbard outside glacier forelands. His traps had a sticky rim to avoid crawling into the trap. Interestingly, the airborne transport of springtails seemed to occur at low wind speeds and in periods with high air humidity, indicating a high surface activity during such conditions. Since springtails can jump, they may be taken further by air currents. In Alaska, wind-blown springtails and mites have been collected in suspended plankton nets (Gressitt and Yoshimoto 1974). Elsewhere, they have even been taken as aerial plankton at altitudes of 1,500 m (Glick, 1939; Riley et al., 1995), so local dispersion by wind seems likely.



Fig. 6. Sticky trap illustrating activity of various Diptera on a 3 year old moraine at Midtdalsbreen glacier snout, Norway. Photo: Sigmund Hågvar.

Most beetles can fly, but not all. Not surprisingly, typical pioneer beetles are generally fully winged, while non-flying species are late colonisers in glacier foreland (Gobbi et al., 2007). However, dispersing by foot may be efficient in certain very active invertebrates, as the large Opiliones of the genus *Mitopus*, mentioned above.

The combined knowledge today indicates that pioneer communities in glacier forelands are rather predictable, and that dispersal may not seriously restrict community development (e.g. Hodkinson et al., 2004; Kaufmann, 2001; Vater, 2006). However, this does not mean that pioneer species have to be ecologically similar.

5. Ecological similarities and differences between pioneer invertebrates

5.1 Specialists or generalists?

Pioneer invertebrates in European glacier forelands comprise both specialists and generalists. Even specialists represent a heterogeneous group, depending on their speciality. Some are "cold-loving", represented by the springtail *Agrenia bidenticulata* (Hågvar, 2010) and certain carabid beetle species of the genus *Nebria*, for instance *Nebria nivalis* (Bråten & Flø, 2009; Gobbi et al., 2007; Kaufmann, 2001; Vater, 2006). Such cold-adapted species may increase their distribution if the area of pioneer ground increases due to an increased melting rate, but may eventually disappear locally if the glacier or snow field melts away. A second group of specialists are those preferring open, barren ground. Some of these, both among microarthropods, beetles and spiders, have an alpine and/or arctic distribution. However, some also occur in lowland areas on various sandy, gravely or stony habitats, for instance carabid species of the genus *Bembidion* (Bråten & Flø, 2009) or the springtail species *Bourletiella hortensis* (Hågvar, 2010).

Ecological generalists from several taxonomic groups are found in pioneer communities. These species tolerate a wide range of habitats, both in the lowland and in mountains. Examples from European glacier forelands are the carabid beetle *Amara quenseli*, the harvestman *Mitopus morio*, the springtail *Isotoma viridis*, and the oribatid mite *Tectocepheus velatus* (Bråten & Flø, 2009; Hågvar, 2010; Hågvar et al., 2009; Hodkinson et al., 2004; Kaufmann, 2002; Vater, 2009). An interesting point is that it is rather predictable which "generalists" are present among the pioneers, in the same way as the specialists are predictable. Clearly, only a few "generalists" can extend their ecological niche far enough to thrive on pioneer ground close to a glacier – including the ability to arrive there. Later successional stages may contain several other "generalist species", but they do not have this extra flexibility.

5.2 Parthenogenetic or bisexual?

Some springtails and mites are parthenogenetic, which means that one single individual can start a local population. This ability is an obvious advantage for a pioneer species if dispersion is a limiting factor. In a glacier foreland in south Norway, Hågvar et al. (2009) found that the two characteristic pioneer mites were parthenogenetic. However, parthenogenetic mites were found along the whole foreland gradient, including some slow-dispersing species. Among springtails in the same foreland, the pioneer species were mainly bisexual (Hågvar, 2010). Therefore, among microarthropods, parthenogenesis is not more typical among pioneer species than among later colonisers. This may indicate efficient dispersal of individuals.

5.3 Short or long life cycle?

Pioneer species with a short life cycle might have an advantage compared to species with a long life cycle in establishing a high and permanent population. Most of the typical pioneer springtail species in alpine south Norway have a one-year life cycle, which is relatively “fast” under these conditions (Fjellberg, 1974; Hågvar, 2010). However, the pioneer oribatid mite *Tectocephus velatus*, is assumed to use two or more years to fulfil the life cycle in the same area (Solhøy, 1975). This species was represented mainly with juveniles in the pioneer site at Hardangervidda, indicating local reproduction (Hågvar, 2010). For this species, a slow development does not seem to be a handicap in colonisation and establishment.

5.4 Resident survivors or continuously colonising?

High densities of pioneer microarthropods could be due to continuous transport by air. Theoretically, the pioneer ground might be an ecological sink, receiving animals which continuously die. However, filled guts in sampled microarthropods indicate feeding activity on the pioneer ground. Whether pioneer ground may to a large degree be a sink for ballooning spiders, is an open question.

5.5 Saprophagous super-pioneers?

In a glacier foreland in the Austrian Alps, Bardgett et al., (2007) found that pioneer, heterotrophic microbial communities to a large degree used ancient carbon released by the glacier as an energy source. Only after more than 50 years of organic matter accumulation did the soil microbial community change to one supported primarily by modern carbon, most likely from recent plant production. This means that also pioneer microarthropods feeding on fungi and bacteria could use ancient carbon, allowing microarthropods to establish resident populations immediately after the ground is laid free of ice. Inblown organic material will also gradually add substrate for saprophagous food chains. Microbial-feeding animals like microarthropods, rotatoria, tardigrada, nematoda and enchytraeidae may be the first animals which establish viable and resident populations independently of resources from outside. If so, they are the super-pioneers among animals.

6. The predator first- hypothesis

According to conventional ecological textbooks, a primary succession should start with the establishment of plants. These would offer life conditions for herbivore animals, which finally allow the presence of predators. Hodkinson et al. (2002) showed that in practice, newly exposed substrates, as a fresh glacial moraine or a cooled volcanic lava flow, are to a large degree inhabited by various predator invertebrates. In other words, the autotrophs are preceded by a largely unrecognized heterotrophic phase. Summing up literature documenting aerial transport and deposition of invertebrates, they assumed that pioneer predators were fed by a fallout of invertebrates onto land and water surfaces (Figs. 6-7). In addition, a fallout of detritus would favour scavenging detritivores. It was suggested that these heterotrophic communities conserve nutrients, particularly nitrogen, and facilitate the establishment of green plants. In a glacier foreland on Svalbard, Hodkinson et al. (2001) showed that spider densities were highly correlated with allochthonous inputs of potential prey items, predominantly chironomid midges. Coulson et al. (2003) further documented aerial transport of invertebrates in the same foreland.

Pioneer foreland communities containing macroarthropod predators have been documented both on Svalbard, in Norway, and in the Alps (Bråten & Flø, 2009; Gobbi et al., 2006a,b, 2007; Hodkinson et al., 2004; Kaufmann, 2001; Kaufmann & Raffl, 2002; Vater, 2006). While spiders represent the pioneer predators on Svalbard, a mixture of carabid beetles, various spiders and one or two harvestman species are typical on the European mainland.



Fig. 7. Air-borne insects sampled on the surface of the Hardangerjøkulen glacier, south Norway. These specimens have been a part of the air plankton, but low temperatures above the glacier have made them fall down. Photo: Marte Lilleeng.

6.1 The predator first-hypothesis challenged

The predator first-hypothesis is at first sight an ecological paradox, but can be explained if the predators are fed by airborne food as for instance chironomid midges. But how stable is the airborne input of suitable and sufficient food to the pioneer ground? As already pointed out by Hodkinson et al. (2002), detritivores such as *Collembola* can also be eaten by predators such as spiders and carabid beetles. But to what degree is this occurring, and how important are resident *Collembola* or mite species as a stable food source? Gut content analyses are needed to answer these questions, preferably by recognizing prey items via their specific DNA. Perhaps the input of predators is very high, for instance of ballooning spiders, and that predators to a large degree eat other predators? Are pioneer sites in practice large sinks, where the majority of even predators do not survive? And which of the pioneer beetles, spiders and harvestmen do really reproduce on the barren ground?

Recent studies in the foreland of Midtalsbreen glacier snout, south Norway, indicate that chlorophyll-based food chains may start very early. Interestingly, the key organisms in this respect are mosses. On a large moraine which was freed from ice in 2005, twenty pitfall

traps were operated during the snow-free season 2008. Besides a pioneer fauna of beetles, spiders and harvestmen (Bråten and Flø, 2009), mites and springtails, the traps contained inblown fragments of various mosses. These fragments, among them so-called bulbils (Fig. 8) are able to develop into moss colonies. However, because these diaspores are tiny and end up between stones and gravel, they are not visible by eye in the field. By studying the gut content of springtails in the traps, it was revealed that most individuals of the large, sphere-formed species *Bourletiella hortensis* had eaten leaves and/or rhizoids of mosses (Figs. 9-10). This species can be very active and was observed to make jumps up to 10 cm length on the moraine, so it can obviously locate the inblown moss fragments. If the predatory beetles, spiders and harvestmen can eat this species, chlorophyll-based food chains may start very early.



Fig. 8. Certain mosses can easily be wind-dispersed by so-called bulbils. This picture shows how individual moss plants, including rhizoids, develop from bulbils placed on moist plaster of Paris. Photo: Sigmund Hågvar.

The first moss patches may also serve as a habitat for certain moss-living macroinvertebrates. After four years, in 2009, dry extraction of a small moss patch on the moraine revealed two larvae of terrestrial Chironomidae, as well as larvae and a pupa of the beetle *Simplocaria metallica* (Byrrhidae). The pupa soon hatched in the laboratory. Few insects are moss-eaters, but the family Byrrhidae is an exception (Figs. 11-12). The importance of mosses for early faunal succession in glacier forelands should be closer studied. Maybe pioneer mosses represent a “driver” which facilitates the colonisation of certain invertebrates.

It should also be noted that some pioneer carabid beetles in the genus *Amara* are considered to be omnivorous, for instance *Amara quenseli* and *Amara alpina* (e.g. Lindroth, 1986) and these might for instance feed on inblown seeds.



Fig. 9. Three specimens of the moss-eating springtail *Bourletiella hortensis*. An inblown moss fragment of 1 mm length is in the middle. Photo: Marte Lilleeng.

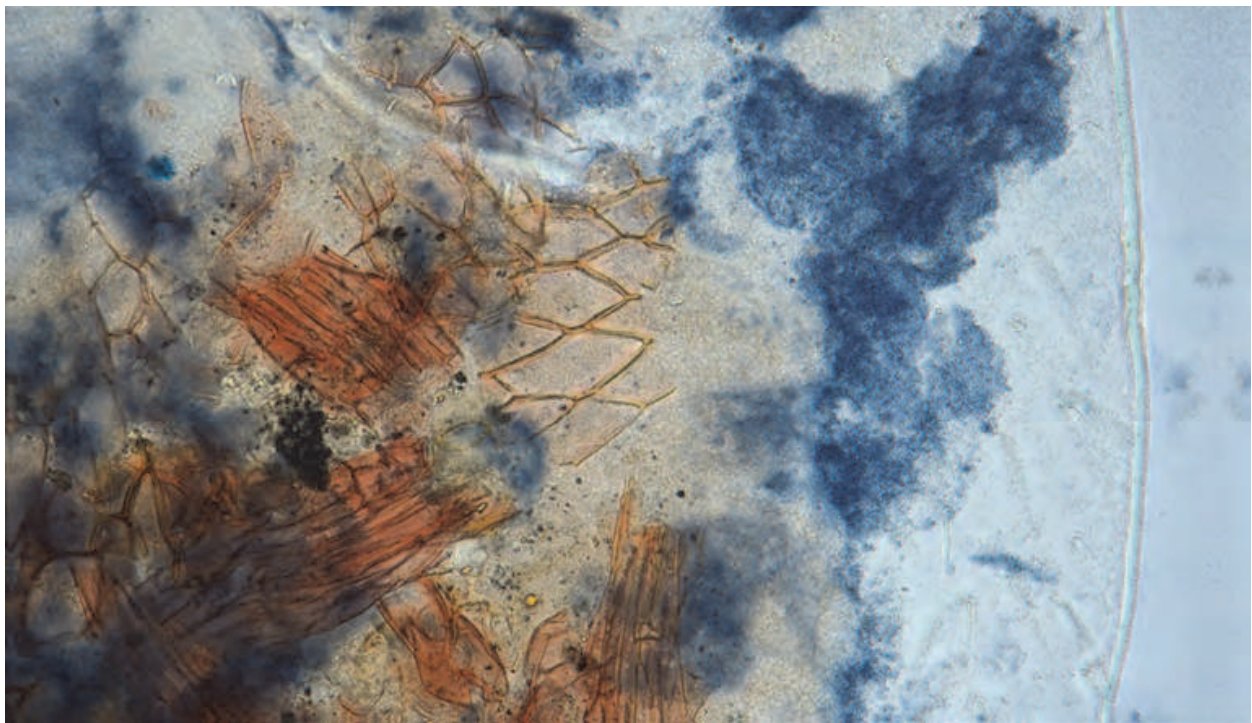


Fig. 10. Gut content of the springtail *Bourletiella hortensis* showing brown moss fragments. Photo: Marte Lilleeng.

7. A new look at pioneer communities?

The predator first-hypothesis is valuable by pointing to the fact that many predators are present rather immediately, before any visible primary production. Their food requirements can probably be fulfilled by aerial transport of invertebrates. But animal life on a young moraine is more complicated than that. The super-pioneers among animals are microflora-feeding groups belonging to the decomposer food chain, and some of these may serve as food for predators. Furthermore, certain moss-eating microarthropods, beetles and Chironomidae are present after few years, being part of chlorophyll-based food chains.



Fig. 11. Newly hatched adult and larva of the moss-eating beetle *Simplocaria metallica*. Photo: Marte Lilleeng



Fig. 12. Pioneer moss patch after four years. Midtdalsbreen glacier snout, south Norway. Photo: Sigmund Hågvar

Maybe also cyanobacteria with chlorophyll are present very early. Some of the typical pioneer beetles are omnivorous and may eat inblown seeds. Finally, who eats who is still an open question, as well as whether pioneer ground is a sink or a reproduction ground. The ecology of pioneer communities may be more complicated than earlier thought



Fig. 13. This rim of pioneer mosses along a large stone after four years is due to inblown moss fragments which have aggregated along the stone. Midtdalsbreen glacier snout, south Norway. Photo: Sigmund Hågvar.

8. Succession patterns after the pioneer stage

The succession from a pioneer stage to a mature, stable community goes through various phases which are more or less predictable. Not surprisingly, both the botanical and the zoological succession can be related to three more or less interrelated factors: Time since glaciation, distance to glacier and vegetation cover (e.g. Bråten & Flø, 2009; Gobbi, 2007; Hågvar, 2010; Hågvar et al., 2009; Hodkinson et al., 2004; Kaufmann, 2001; Matthews, 1992; Vater, 2006). In the zoological succession, an obvious element is that herbivores like Chrysomelidae and Curculionidae have to wait for their host plant to be established. Furthermore, certain microarthropods and saprophagous beetles depend on a certain thickness of the soil organic layer (Bråten & Flø, 2009; Hågvar, 2010; Hågvar et al., 2009). Different taxonomic groups may show different succession patterns in the same foreland. For instance, at the Midtdalsbreen glacier foreland in south Norway, springtails colonised faster than oribatid mites. After 70 years, 84 % of the springtail species in the chronosequence were present, but only 57 % of the oribatid mites (Hågvar, 2010; Hågvar et al., 2009). Beetles followed a pattern similar to springtails, while spiders colonised more gradually, similar to oribatid mites (Bråten & Flø, 2009). The general rate of succession can also differ between geographical sites. In the foreland of the Rotmoos glacier in Austria, most beetle and spider species were present after only 40-50 years (Kaufmann, 2001). This is

a faster colonisation rate than observed in alpine south Norway (Bråten & Flø, 2009; Vater, 2009). The difference is probably due to a milder climate in the Austrian site, since certain taxa absent in the Norwegian sites were present there, e.g. Lumbricidae, Formicidae, and Diplopoda.

In an extensive study of eight different glacier forelands in south Norway, Vater (2006) demonstrated how altitude and local climate influenced colonisation rate, even within a small geographical area. In the forested sub-alpine zone the colonisation rate of macroarthropods was high, while the succession was very slow in a high alpine foreland. A “geoecological model” was proposed by Vater (2006) to explain three distinctive pathways of succession, representing the subalpine, the low/mid-alpine, and the high alpine zone, respectively. Certain characteristic species could, however, be pioneers at very different altitudes.

Although the colonisation rate may vary considerably between sites due to climatic differences, the sequence between different taxa or ecological groups may show striking similarities. We see that both within south Norway, and in comparison with the Alps (Bråten & Flø, 2009; Kaufmann, 2001; Kaufmann & Raffl, 2002; Vater, 2009). Among beetles, surface active predators within the family Carabidae are typical pioneers, while the species-rich family Staphylinidae dominates later. This family contains many small species which are favoured by the development of an organic soil layer. Most herbivorous species are also relatively late colonisers, except for the moss-eating genus *Simplocaria* (Byrrhidae), which can inhabit pioneer moss patches. An interesting aspect is that herbivore beetles do not necessarily colonise promptly when the food plant is established. In the Midtdalsbreen foreland, *Chrysomela collaris* (Chrysomelidae) was found after about 80 years, while the food plant *Salix herbacea* belonged to the pioneer species. The explanation may partly be that the beetle is a slow disperser, partly that a certain cover of the food plant is needed.

From the Alps, Kaufmann (2001) concluded that faunal colonisation and succession in alpine glacier forelands, to a large extent, followed predictable and deterministic assembly rules and that stochastic effects were of minor importance. Studies in Norway and Svalbard support this general picture. However, Kaufmann (2001) also stressed that favourable sun and light conditions may facilitate successional progress in local patches.

A general question in succession studies is the turnover rate of species. To answer this, most species have to be identified. Based on a limited taxonomical resolution, Vater (2006) concluded that most macroinvertebrates remained after colonisation. However, in the Alps, several pioneer species of spiders and beetles were absent in later successional stages (Gobbi, 2006b, 2007; Kaufmann, 2001). Bråten & Flø (2009) found that most spiders remained after colonisation, while beetles showed a certain turnover of species. Within mites and springtails, most species remain after colonisation, although their abundance and relative dominance may vary throughout the chronosequence (Hågvar, 2010; Hågvar et al., 2009).

9. Climate change and succession pattern

A gradually warmer climate will make it more difficult to use dated sites as a substitute for time. Kaufmann (2002) concluded that an increase of 0.6°C in summer temperatures approximately doubled the speed of initial colonisation, whereas later successional stages were less sensitive to climate change. It is also possible that the surrounding source habitats may be influenced and increase their dispersion of species into the foreland.

Since the first effects of climate change are likely to be observed in terrestrial habitats at northern latitudes (IPCC, 2007), Norwegian studies may be especially relevant. Alpine areas of southern Norway have both had a marked temperature increase during the last 2-3 decades, and been subject to deposition of long-distance transported atmospheric nitrogen (Hole & Engardt, 2008; Ytrehus et al., 2008). Fertilization effects are most probable in nutrient-deficient ecosystems, such as alpine habitats with poorly developed soils. In a nutrient poor alpine *Dryas* heath in south Norway, experimental plots were artificially heated and/or fertilized to study the combined above-ground (plants) and below-ground (soil animals) effects (Hågvar & Klanderud, 2009). Nutrient addition and nutrient addition combined with warming resulted in several effects below ground on microarthropods as previously shown above ground on plants: Increased biomass, high dominance of a few rapid-growing species, contrasting responses of closely related species, and a reduction in species numbers. An earthworm (*Dendrobaena octaedra*) which was very rare in control plots, seemed to be favoured by the changes. These short-term responses (after 4 years) may have profound long-term effects in this alpine ecosystem.



Fig. 14. Pitfall trap on a three year old moraine with several specimens of the predacious and very active Carabidae species *Bembidion hastii*. But what is the density of the species, what does it eat, and does it reproduce here? Photo: Sigmund Hågvar.

10. Future research

Although we are beginning to understand several trends and mechanisms in the primary succession of glacier forelands, more field studies with a high taxonomic resolution, and from different geographical areas, are needed. It is a special challenge to explain the ecological mechanisms working in pioneer communities on barren ground. What is the importance of pioneer microflora as food for pioneer microarthropods, and how important are resident microarthropods as food for pioneer beetles and spiders? Gut content analyses based on DNA primers of potential prey items would be highly welcome. And how important are pioneer mosses as a driver in succession?

Another improvement would be to add more quantitative samplings methods. Pitfall trapping favours fast-moving surface species (Fig. 14). Species with low densities may give considerable catches if they are very active, while species with higher densities may be lacking in the pitfall traps if they are rather immobile (for instance web-building spiders or moss-eating beetles).

Long-term monitoring of selected plots can illustrate effects of changed climate on succession. Plots which are already well studied should be re-studied at intervals. A better understanding of primary succession makes it easier to forecast what future ecosystems may be like in areas freed from ice. It can also increase our general insight into ecology, maybe by removing the “predator first-paradox” as a paradox.

11. Conclusion

Due to global warming, glaciers are receding in many parts of the world, leaving considerable areas of barren ground. While the botanical succession in such glacier forelands have been well studied, the parallel zoological succession is less described and understood. Glacier forelands illustrate nature’s ability to recover from severe disturbance, and it is of considerable ecological interest to understand the succession process. Succession studies also help us to predict future ecosystems in deglaciated terrain.

This chapter summarizes and compares zoological studies in glacier forelands within three main areas in Europa: Svalbard, south Norway, and the Alps. A common technique is to study sites with known age in different distances from the ice. The sequence of dated study plots is called a chronosequence, and the various plots act as a substitute for following the same plot over time. Not surprisingly, time, distance and vegetation cover use to be highly correlated factors in a glacier foreland.

Several invertebrates are present before any vegetation is visible. Typical representatives are springtails (Collembola), mites (Acari), beetles (Coleoptera), spiders (Araneae), and harvestmen (Opiliones). The actual species are surface active animals, but they find shelter in the crevices among stones, gravel and sand grains. Springtails and mites are saprophagous, while species from the other groups are mainly predators. It has been called an ecological paradox that predators precede both plant-eaters and plants. However, the pioneer ground receives airborne insects (mainly Diptera), on which the predators can feed. This fertilizes the ground and contributes to the gradual establishment of plants. However, chlorophyll-based food chains may start surprisingly early, for instance based on pioneer mosses on which certain springtails and beetles can feed.

In the Alps, most arthropod species colonise during a period of 40-50 years, while the colonisation is slower in Norway. High Arctic forelands on Svalbard have a poor fauna, but

springtails, mites and certain spiders are early colonisers even there. Certain invertebrate taxa are typical pioneers in all three geographical areas, or common to Norway and the Alps. It is also concluded that the main pattern of the zoological succession is rather predictable. This indicates that dispersion may not be a serious problem. Herbivorous invertebrates are often relatively late colonisers.

Some pioneers are highly specialised, cold-tolerant species. These may go locally extinct if the glacier melts away. Other are open ground-specialists, and may live also in open habitats in the lowland. Several are generalists, with an extra flexibility to inhabit the harsh conditions close to a glacier. Pioneers may be parthenogenetic or bisexual, or have a short or long life cycle. Although pioneer species form an ecologically heterogeneous group, the pioneer community is often rather predictable.

Some of the remaining questions are: Is dispersal such an easy task? What do the various pioneer species eat? Is the pioneer ground an ecological sink, continuously fed from outside? How do plants and animals interact through succession? More field studies with a high taxonomic resolution, and in various geographical areas, are welcomed. Climate change may generally speed up the succession rate around melting glaciers.

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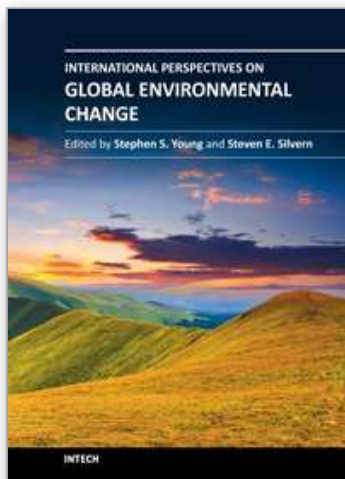
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International Perspectives on Global Environmental Change

Edited by Dr. Stephen Young

ISBN 978-953-307-815-1

Hard cover, 488 pages

Publisher InTech

Published online 03, February, 2012

Published in print edition February, 2012

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Sigmund Hågvar (2012). Primary Succession in Glacier Forelands: How Small Animals Conquer New Land Around Melting Glaciers, International Perspectives on Global Environmental Change, Dr. Stephen Young (Ed.), ISBN: 978-953-307-815-1, InTech, Available from: <http://www.intechopen.com/books/international-perspectives-on-global-environmental-change/primary-succession-in-glacier-forelands-how-small-animals-conquer-new-land-around-melting-glaciers>

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